Chapter seven

7

Contrasting effects of large herbivores on nitrogen mineralization across ecosystems: integrating effects of soil physical properties.

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Abstract

The general view of the role of large herbivores in grassland ecosystem functioning is that they speed up nutrient cycling, especially nitrogen (N) mineralization. This classic 'grazing lawn' effect is thought to arise because faecal and urine inputs by herbivores increase soil microbial activity and thus N mineralization, which promote plants with leaf N concentrations, which finally again attracts herbivores. However, field experiments increasingly show that large herbivores often reduce soil N mineralization rates instead of increasing them.

We explain this through effects of large herbivores on soil physical processes, which under some conditions are found to outweigh positive effects on N mineralization. We expect these effects to be strongest in wet, fine-textured soils. In such soils compaction causes periods of soil hypoxia during which aerobic decomposers (both microbes and soil macrofauna) are inhibited which may result in a reduction in N mineralization.

We use long-term field data from experiments in temperate grasslands with different grazing and mowing treatments to substantiate this proposed role of soil compaction in slowing N turnover and promoting soil hypoxia. These experiments reveal that plant species adapted to periods of soil hypoxia and to low N availability generally have higher abundances in more compacted soils.

We conclude that the effect of large herbivores on N mineralization depends on a critical balance between a set of positive and negative effects. Including herbivore effects on soil physical properties into current theories on N cycling in grassland will advance our understanding of contrasting results of herbivores on mineralization rates.

Introduction

Large vertebrate herbivores play a key role in determining the community structure and functioning of grassland ecosystems. They influence nitrogen (N) mineralization rates, thereby altering plant productivity (Georgiadis et al. 1989, Frank and McNaughton 1993, Frank et al. 2000), as this is often limited by N availability (Schlesinger 1991, Vitousek and Howarth 1991). The prevailing theory is that large herbivores locally enhance the productivity of grasslands through promoting N mineralization. As herbivores enhance the primary production and improve grass quality of the grass, which again attracts more herbivores, this can be viewed as a grazer-induced positive feedback loop on their own density (McNaughton 1984, Pastor et al. 2006). Increased N availability caused by large herbivores has therefore been proposed as a form of self-facilitation where herbivores improve the availability and quality of their food plants in specific locations that are inherently not very different from their surroundings (McNaughton 1984, Belsky 1986, Fryxell 1991, McNaughton et al. 1997a). Indeed, several studies where large herbivores were excluded from plots demonstrate a decreased availability of N in the absence of large herbivores (McNaughton et al. 1997b, Frank and Groffman 1998, Knapp et al. 1999). However, other field studies show an increase of N mineralization in the absence of large herbivores (Pastor et al. 1993, Ritchie et al. 1998, van Wijnen et al. 1999, Bakker et al. 2004), indicating that the positive feedback loop of herbivore-induced increased N availability is not universal.

Several authors have tried to explain contrasting effects of herbivores on N mineralization as a function of herbivore-induced changes on the quality of resources entering the soil food web (Pastor et al. 1993, Hobbs 1996, Ritchie et al. 1998, Pastor et al. 2006). Yet field tests could not confirm the predictions of these theories (Bakker et al. 2006, Bakker et al. 2009). Apparently, the effect of large herbivores on N mineralization in grasslands is still not fully understood.

Existing hypotheses on contrasting effects of grazing on N cycling in natural grasslands have so far largely ignored the physical effects of large herbivores on soil parameters. For example by trampling and the removal of aboveground plant biomass herbivores can have an important influence on e.g. soil moisture, soil aeration and soil temperature. Changes in these soil properties may have major consequences for nutrient cycling, and hence for plant productivity and plant N concentrations, and thus again for herbivores attraction. Recent evidence suggests that this may be a promising avenue for explaining many of the seemingly contradictory results (Sankaran and Augustine 2004, Hamza and Anderson 2005, Startsev and McNabb 2007, Sørensen et al. 2009). Empirical studies that have taken trampling effects of herbivores into account have done so in a very narrow window of abiotic soil parameters and have therefore not been able to show effects on N cycling (Curll and Wilkins 1983, Mikola et al. 2009). Here we propose a general framework that

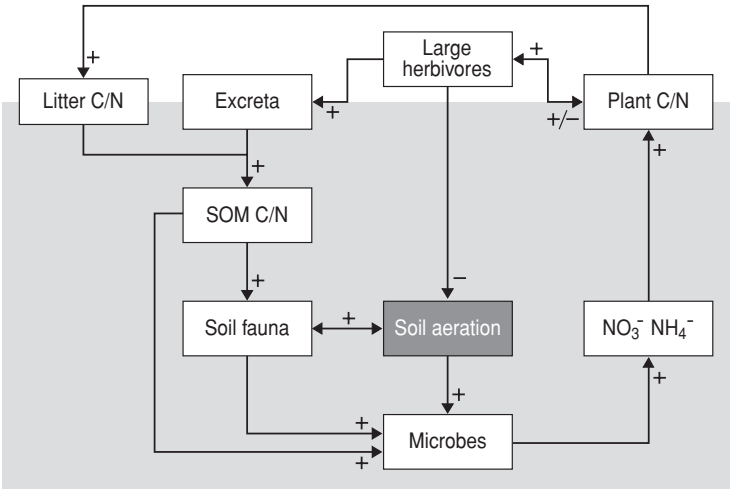

Figure 7.1 Overview of the influence of large herbivores on the nitrogen (N) cycle in grasslands. This diagram depicts three main pathways via which herbivores can influence soil N mineralization. Prevailing theories mainly focus on the two pathways via which herbivores alter the quality of resources entering the soil food web, i.e., by excreting dung and urine and by changing plant quality. The third pathway focuses on herbivore effects on soil physical properties. For example, trampling-induced soil compaction may decrease aeration and consequently alter soil N mineralization. In this figure we integrate the three pathways which will lead to a better understanding of N cycling in terrestrial ecosystems.

incorporates effects of herbivores on soil physical parameters into current theories of N cycling (Fig 7.1). This will advance our understanding of contrasting results of grazing on N mineralization rates in natural grasslands. To illustrate how large herbivores can modify N cycling by means of trampling induced soil compaction, we use data on soil parameters and vegetation composition from long term field experiments.

Explaining contrasting effects of herbivores on mineralization

Several mechanisms have been suggested to explain contrasting effects of large herbivores on N mineralization (see Fig 7.1). The main focus has been on herbivore effects on the quality of resources entering the soil food web. First, herbivores may speed up or slow down N mineralization by returning excreta to the soil. On the one hand, herbivore excreta provide easily available N which stimulates the activity of soil microbes (McNaughton et al. 1997a, 1997b). On the other hand, herbivores return N in different forms, i.e. as urea and faeces which have different decomposition rates, also dependent on microclimate conditions (Hobbs 1996). Urea provides rapidly degradable N, whereas faeces are much slower to decompose, sometimes even slower than plant detritus. Therefore, N excreted in faeces may reduce N mineralization rates (Pastor et al. 2006).

Second, a combination of plant quality and herbivore selectivity may explain contrasting results of herbivores on N mineralization (Ritchie et al. 1998, Pastor et al. 2006). When quality of the dominant plant species is high, herbivores can forage unselectively and return N in urea, which favours growth of fast-growing grazing-tolerant plants (Olff and Ritchie 1998). This can lead to the formation of grazing lawns and to a general increase in N mineralization. However, when the dominant plants are of poor quality, herbivores selectively feed on the high quality subordinate species (as legumes vs. grasses in grasslands, or deciduous tree saplings vs. conifers in forests), which then leads to a shift in community composition towards poor quality species (Pastor et al. 2006). A decrease in plant quality will lead to reduced litter quality and hence may slow down decomposition and mineralization rates (see Table 7.1, Berendse et al. 1989, Wardle et al. 2004, Bardgett 2005). Consequently, herbivores may affect N mineralization in contrasting ways along a gradient of soil fertility. At high fertility sites, where plant quality is high, herbivores may change community composition through inducing a positive feedback on their own abundance by increasing N mineralization and at low fertility sites with low plant quality they may induce a negative feedback (Pastor et al. 1993, Ritchie et al. 1998, Augustine et al. 2003). Whereas examples can be found that support this theory (Pastor et al. 1993, Ritchie et al. 1998), contrasting results are found in other studies. For example, at sites with high soil fertility and high plant quality, such as salt marshes and river floodplains, herbivores have been shown to reduce N mineralization instead of improve it (van Wijnen et al. 1999, Bakker et al. 2004). Hence, both mechanisms described above do still not satisfactorily explain contrasting effects of herbivores on N cycling and neither explicitly take effects of large herbivores on soil physical parameters into account.

Changes in soil physical properties can have a major influence on nutrient mineralization (Hamza and Anderson 2005, Startsev and McNabb 2007) and the effects may be dependent on environmental conditions. For example, in arid environments biomass removal by herbivores can reduce plant cover and litter input to the soil, which may lead to reduced water holding capacity of the soil and increased soil evaporation (van de Koppel et al. 1997). Moreover, in these systems soil compaction by trampling can reduce infiltration of water into the soil. Consequently, in arid environments soil organic matter and water may become limiting for N mineralization in grazed conditions. Herbivores may also affect soil temperature by modifying the insulating capacities of the vegetation through the removal of biomass (Gornall et al. 2009). In cold systems reduced vegetation cover may lead to cooling down of the soil in cold periods, thereby decreasing N mineralization, while in warm periods, soils with low vegetation cover may heat up quickly, which favours mineralization. These examples show that herbivores can modify soil physical properties, which can have important consequences for soil N cycling.

Therefore, we propose that adding herbivore impact on soil physical properties to current models of herbivore effects on N mineralization rates will strongly improve our understanding of the contrasting effects of herbivores on N mineralization (Fig 7.1). From here onwards we will discuss our proposed integrated approach using consequences of soil compaction in temperate grassland as an example showing how this integrated approach may advance our understanding of N cycling in grazed ecosystems.

How trampling-induced soil compaction can reduce N mineralization in grasslands

In every soil some pores will contain water and others will contain air. The amount of water a soil can hold depends on many different factors. Water holding capacity is increased when clay and organic matter content are high or when the fraction of small pores is large (see Bardgett 2005). When soils get compacted, for example as a result of trampling by large herbivores, pore size is reduced, which enhances the fraction of small pores and hence increases water holding capacity (Wolkowski 1990). Generally, when more than 60% of pores are water-filled, diffusion of oxygen is severely hampered because diffusion in water happens 10,000 times slower than in air (Russell 1973). Consequently, in compacted soils oxygen may become limiting for microbial processes, but also for soil fauna and metabolism of plant roots. This may lead to lower N availability because on the one hand nutrient mineralization is slowed down (Breland and Hansen 1996, Jensen et al. 1996, De Neve and Hofman 2000) and on the other hand because denitrification is sped up under anaerobic conditions (e.g. Haunz et al. 1992, De Klein and Van Logtestijn 1994, Lipiec and Stepniewski 1995). Wollersheim et al (1987) showed experimentally that increased bulk density resulted in reduced soil aeration which led to elevated soil moisture levels and denitrification rates.

As the amount of small pores increases in compacted soils, pores available to soil fauna are reduced (Breland and Hansen 1996). Moreover, organic material and microbial biomass become physically protected against attack by soil fauna and microbial feeders, respectively (Breland and Hansen 1996). Consequently, soil fauna densities are found to decrease in more compacted or trampled soils (Whalley et al. 1995, Bouwman and Arts 2000, Sørensen et al. 2009). Higher trophic level soil fauna do not directly mineralize nutrients, i.e. convert organic matter into inorganic forms, but they may affect mineralization rates of microbes and hence the availability of mineral nutrients in the soil (Table 7.1, Osler and Sommerkorn 2007). Several studies report a contribution of soil fauna to nutrient mineralization rates (Verhoef and Brussaard 1990, de Ruiter et al. 1993, Bardgett and Chan 1999, Berg et al. 2001). Particularly, in situations where the microbial community is N limited, the contributions of soil fauna to net N mineralization rates may be relatively high (Osler and Sommerkorn 2007).

Table 7.1 Overview of processes determining nutrient mineralization. Direction in which these processes are influenced by soil compaction is indicated using signs.

Factors affecting mineralization	main direction[a]	explanation
Plants		
plant quality	+	enhanced availability of nutrients stimulates decomposer activity a)
oxygen transport through roots	+	marsh plants use aerenchym to transport oxygen, locally increasing bacterial production b)
root exudates	+	input of carbon into the soil causes higher microbial production c)
Large herbivores		
defoliation of vegetation	+	defoliation results in higher root exudation and litter quality causing higher decomposition d)e)
dung and urine production	+	nitrogen in wastes becomes easily available to microorganisms and plants f) g)
changing plant species community	+/-	preferential feeding on high/low quality results in high/low quality vegetation and litter i)
trampling	+/-	+ litter availability to decomposers increases h) - high trampling results in anoxic soil which inhibits decomposition (this paper)
Soil fauna		
increased organic matter availability to microbes	+	soil fauna pellets serve as favourable mineralization setting j)
stimulating mineralization in gut	+	guts of earthworms, termites, microarthropods stimulate soil microbial decomposition k), l)
excreting excess nutrients	+	by foraging on microbes, soil fauna accelerates nutrient mineralization ("microbial loop") m)
bioturbation	+	termites, mice, earthworms, ants create macropores by digging and burrowing activities n), o)
Soil parameters		
soil fertility	+/-	high soil fertility yields high mineralization, low soil fertility leads to lower mineralization p)
compaction in clay soil	-	compaction causes lower soil aeration resulting in high denitrification and low mineralization q)
compaction in sandy soil	+	compaction causes higher litter infiltration and therefore higher nutrient availability to soil detritivores q)
soil moisture	+/-	mineralization works optimal under intermediate moisture conditions. Both in dry and very wet soils mineralization is impeded. r)

[a] Indicates whether mineralization is generally enhanced (+) or decreased (-)

a) (Wardle 1998); b) (Vartapetian and Jackson 1997); c) (Bardgett et al. 1998); d) (Briske et al. 1996); e) (Ferraro and Oesterheld 2002); f) (Afzal and Adams 1992); g) (Bogaert et al. 2000); h) (Zacheis et al. 2001, 2002); i) (Ritchie et al. 1998, Wardle 2002); k) (Trigo et al. 1999); l) (Daniel and Anderson 1992); m) (Clarholm 1985); n) (Lavelle et al. 1997); o) (Brown et al. 2000); p) (Sankaran and Augustine 2004); q) (Rasiah and Kay 1998); r) (Bardgett 2005)

Effects of trampling on plant growth

Soil compaction may have severe consequences for the growth of plants. Most studies report negative effects of grazer-induced soil compaction on plant growth (Abdelmagid et al. 1987b, Menneer et al. 2005, Hamza and Anderson 2005, Drewry et al. 2008). On the one hand, N mineralization rates in compacted soils may be reduced which will result in a decrease in plant production and a higher dominance of plant species performing better on soils with lower N availability. On the other hand physical effects of soil compaction may lead to oxygen limitation and waterlogging, resulting in increased abundance of plant species better adapted to these circumstances. When the available oxygen gets used up by soil microbes other electron acceptors will be used for bacterial metabolism. Anoxic oxidation processes result in a lower redox potential because of the production of reduced compounds (Laanbroek 1990). These compounds (Mn^{2+}, H_2S, Fe^{2+}) together with the lack of oxygen may severely harm root metabolism. This often leads to root death (Jackson and Armstrong 1999), sometimes within a few hours (Elzenga and van Veen 2010). Plant species may adapt to hypoxia and waterlogging in compacted soils by forming aerenchym, which serves as an alternative pathway for supply of oxygen to the root other than diffusion through soil pores (Table 7.1, Jackson and Armstrong 1999). Consequently, on wet soils that have been compacted, we expect an increase in plant species with aerenchym in their roots, as well as a shift towards plants performing better under conditions of lower nutrient availability.

Soil compaction along environmental gradients

Effects of soil compaction on nitrogen mineralization are often reported to be negative (Hamza and Anderson 2005). However, the strength and direction of soil compaction effects depend on different soil properties including soil type and soil moisture content (Table 7.1, Kiehl et al. 2001, Hamza and Anderson 2005). Therefore, contrasting effects of herbivores on N mineralization may be explained by contrasting effects of large herbivores on soil compaction along environmental gradients of soil type, rainfall and temperature.

In sandy soils, compaction may enhance soil nutrient availability as a result of higher nutrient diffusion rates (Voorhees et al. 1985, Rasiah and Kay 1998, Xu et al. 2008), less leaching of nutrients (Xu et al. 2008) and better water retention. The positive consequences of compaction in sandy soils become negative when considering soils that are rich in silt and clay (Rasiah and Kay 1998), because fine-textured soils are much more compactable by trampling than sandy soils. This yields an interesting effect where the positive effects of finer texture on nutrient availability can be undone by the negative effects of soil compaction under grazing. Soil moisture content is also an important determinant of effects of soil compaction on nutrient cycling. In very dry soils herbivores may enhance water availability because compaction may increase water retention and disturbances of the soil top

layer can increase water infiltration (Abdelmagid et al. 1987a) which results in higher mineralization rates. In contrast, in wet soils compaction may reduce oxygen availability thereby decreasing mineralization rates. The effect of soil type often interacts with hydrological conditions, because clay and peat soils commonly occur under wetter conditions (e.g. high groundwater tables, flooding) than sandy soils.

The effects of soil compaction can be organized along the axes of soil type and soil moisture. Across these axes, soil compaction in dry and sandy soils has small, stimulating effects on N mineralization. In wet and clay soils effects will be larger because they are more susceptible to compaction and compaction will often lead to a reduction of N mineralization. Consequently, we expect that the effect of trampling-induced soil compaction on mineralization rates varies across environmental gradients. Trampling may have little or no effect on mineralization in habitats with non-compactable sandy soils, while they may strongly reduce mineralization on wet and clayey soils.

Herbivore effects on plant community composition through modification of soil physical properties– examples

Empirical studies that try to explain contrasting results of herbivores on N cycling in natural systems through herbivore effects on soil physical properties are still lacking. Most recent studies that have attempted to quantify the relative importance of soil compaction on N mineralization rates focused on agricultural systems with supposedly proper drainage facilities (Curll and Wilkins 1983, deBruyn and Kingston 1997, Mikola et al. 2009). However, effects of soil compaction via waterlogging and oxygen limitation on plant communities may play a more important role in areas without artificial drainage. Therefore, we analyzed data from existing long-term management experiments in Dutch grassland systems to get first insight in effects of herbivores on soil compaction and hence on plant community composition. From the plant community responses we aim to imply the consequences for N mineralization, as these were not directly measured in these studies. We specifically address (1) how herbivores affect soil compaction, (2) how increased soil compaction results in a shift in plant community composition, and (3) what these changes in soil compaction and plant community composition imply for N mineralization rates.

Experimental set up and data analysis

We used data from a grazing experiment on the salt marsh of Schiermonnikoog (53°30'N, 6°10'E), which was set up in the 1970s on a clay soil. We studied soil physical properties and plant community composition in a cattle-grazing treatment (stocking rate 1 cow ha^{-1}), and a hand-mowing treatment. In both treatments aboveground biomass was removed, but the treatments potentially differed in levels of soil compaction. We collected soil cores in 2010 to measure herbivore effects on soil physical properties (Table 7.2). In addition, we used data from three

mowing experiments located in the river valley of the Drentsche Aa (53°N, 6°43'E), also set up around 1970. In these experiments no cattle-grazing treatments were available, but there were plots that were mown with heavy machines and plots that were hand mown. Therefore, we could use these experiments to confirm whether soil compaction affected plant community composition, because on both mowing treatments aboveground biomass was removed, while levels of soil compaction potentially differed. The three sites were located on different soil types, i.e. an organic soil (Lammertshem), a sandy soil (Loefvledder B), and an intermediate (Loefvledder A). Experiments in Loefvledder A and B are still maintained, but the experiment at Lammertshem was terminated in 1983 because the site was rewetted. We collected soil cores in 2010 in Loefvledder A and B to measure soil physical properties in the different mowing regimes. More details on setup of the four field experiments that we used can be found in (Bakker 1989).

In wet areas, like our study sites, soil compaction usually leads to higher soil moisture and hypoxia. Therefore we tested vegetation responses by comparing the cover of aerenchym and non-aerenchym producing plant species in the different management regimes (Justin and Armstrong 1987). For Schiermonnikoog, and the Loefvledder A and B sites we used recent plant cover data (1994-2003) because it may take some time for plant communities to respond to the management regimes. For Lammertshem we used data from 1980-1983 since the experiment was not continued after 1983. To study the potential impact of soil compaction and hypoxia on N mineralization we used Ellenberg indicator values for nitrogen (Ellenberg et al. 1992) for the data from Loefvledder A and B only, because in these sites Ellenberg indicator values are well calibrated and commonly used for wet river valley sites (Ozinga et al. 2009). A shift towards lower Ellenberg N values would indicate a reduction in the cover of nitrophilous plant species and hence may imply lower availability of mineral N in the soil and possibly slower nutrient cycling.

Results

On the salt marsh of Schiermonnikoog we found significantly increased levels of soil bulk density (i.e. the herbivores compacted the soil) in the grazed sites, soil moisture and soil organic matter content (Table 7.2). The plant community responded to the altered soil physical conditions with a shift in community composition. In grazed, i.e. more compacted, plots we found significantly higher coverages of aerenchym producing plant species (Fig 7.2A), which are adapted to periods of low oxygen availability in the soil.

In Loefvledder A we did find increased levels of soil bulk density in machine-mown plots, but differences in weight per volume between soil organic matter and sand masked the much higher degree of compaction probably present at the site

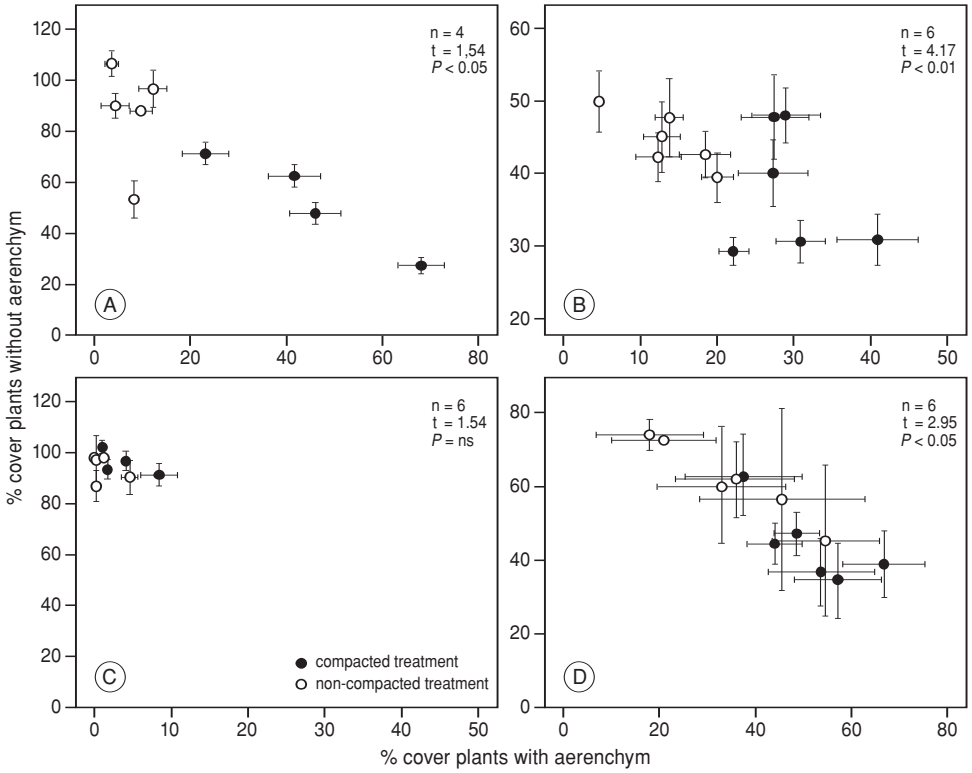

Figure 7.2 Cover of plant species without aerenchym plotted against the cover of plant species with aerenchym in four different study sites under different management regimes and hence different levels of soil compation. a) salt-marsh Schiermonnikoog, b) Loefvledder A in the Drentsche Aa river valley , c) Loefvledder B in the Drentsche Aa river valley, and d) the Lammertshem in Drentsche Aa river valley. Closed circles represent compacted treatments (cattle-grazed or machine-mown) and open circles represent non-compacted treatments (hand-mown). In a), b) and c) each data point represents the average cover of plant species per plot over the last 10 years of the experiments (1994-2003). In d) each data point represents the average cover of plant species over the last 4 years (1980-1983).

Table 7.2 Soil physical properties for Schiermonnikoog in cattle-grazed and hand-mown plots. Values are averages ± standard error. Asterisks indicate level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

	Cattle-grazed	Hand-mown	N	t	
Soil physical properties					
Soil moisture content (%)	55.1 ± 3.6	42.7 ± 4.5	6	3.7	**
Soil organic matter content (%)	8.4 ± 2.4	4.2 ± 0.8	6	2.3	*
Bulk density (g dry weight/ml soil)	0.60 ± 0.05	0.52 ± 0.03	6	4.0	**

(Table 7.3). In Loefvledder B soil physical properties were not different between the management regimes (Table 7.3), probably because this site was situated on a more sandy soil, which is less compactable. The observed soil physical conditions were reflected in the plant community composition. In Loefvledder A (Fig. 7.2B), as well as the Lammertshem (Fig. 7.2D) we found a significant shift towards higher coverage of aerenchym species in machine-mown compared to hand-mown plots, while in Loefvledder B there was no difference between the mowing treatments (Fig 7.2C). Similarly, Ellenberg N indicator values at the Loefvledder A site were significantly lower in machine-mown than in hand-mown plots (Table 7.3), while we did not find a difference in Loefvledder B plots (Table 7.3).

Conclusion of the examples

The long term experiment on Schiermonnikoog shows that herbivores alter soil physical conditions in such a way that lower N mineralization rates are expected; and these changes in soil properties are reflected in the plant community. The analysis of the Drentsche Aa data confirmed that changes in soil physical properties as a result of soil compaction may show up in the plant community. It also showed that cover of nitrophilous plant species was reduced suggesting that N mineralization may be lower in compacted soils. Moreover, it implied that the influence of compacting agents (in this case heavy machines) on levels of compaction, plant community composition, and N mineralization rates depends on environmental conditions like soil type and soil moisture content, because on sandy, thus less-compactable, soils we did not measure a response to soil compaction.

Table 7.3 Soil physical properties and Ellenberg N indicator values for Loefvledder A and B in machine-mown and hand-mown plots. Asterisks indicate level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. We present Ellenberg indicator values as a weighted average per mowing treatment. For each plot we multiplied the N indicator value by the % vegetation cover with that value.

	Machine-mown	Hand-mown	N	t	
Soil physical properties Loefvledder A					
Soil moisture content (%)	73.7 ± 2.3	66.7 ± 2.4	6	7.6	***
Soil organic matter content (%)	46.7 ± 5.2	38.5 ± 4.9	6	4.5	**
Bulk density (g dry weight/ml soil)	0.42 ± 0.05	0.41 ± 0.03	6	0.6	NS
Soil physical properties Loefvledder B					
Soil moisture content (%)	59.7 ± 1.7	59.9 ± 2.6	6	-0.1	NS
Soil organic matter content (%)	13.2 ± 0.9	11.6 ± 1.0	6	2.5	NS
Bulk density (g dry weight/ml soil)	0.67 ± 0.05	0.68 ± 0.05	6	0	NS
Ellenberg N indicator values					
Loefvledder A	17.3 ± 4.5	28.6 ± 1.8	6	-3.5	**
Loefvledder B	36.7 ± 5.2	32.8 ± 4.2	6	0.6	NS

Conclusion

Combination of the modification of soil physical properties by herbivores with the longer known effects of reducing organic matter C/N ratios allows for the understanding of contradictory results observed so far of large herbivore impacts on nutrient cycling in grasslands. An integrated framework allows us to study the relative importance of herbivore effects on nutrient cycling via changes in plant communities, return of dung and urine to the soil and trampling (Fig 7.1). Whether overall effects of herbivores on N mineralization are positive or negative depends on the balance between different mechanisms affecting nutrient cycling (Fig 7.1). When positive effects of grazing on soil organic matter quality via dung, urine and litter return outbalance negative effects via modification of physical properties, we expect an overall increase in mineralization rates. On the other hand, negative effects may outbalance positive effects, for example in the case of trampling on fine-textured soils. We propose that in temperate ecosystems, the outcome of the balance is too a large extent predictable because it depends on the interaction between soil type and soil moisture content. In systems where soils are not very compactable, i.e. systems with dry or sandy soils, it is likely that positive effects of grazing will dominate. In contrast, in systems where soils are compactable, i.e. systems with organic or clay soils, negative effects may be most important. Different effects are expected when large herbivores have strong impacts on soil temperature or drought as in arctic or arid ecosystems, but this requires further analysis. To single out whether changes in plant community composition as a result of soil compaction by herbivores are really related to a lower N mineralization and whether such effects of herbivores are different along gradients of soil compactibility there is a need for field experiments. Such experiments should directly investigate herbivore effects on nutrient cycling, mineralization rates and other soil physical properties in soil types with different susceptibility to compaction.

The framework presented allows us to understand some of the contradictory results in N mineralization that have been found in grasslands previously, but could not be explained with the current theories. Analysis of four long-term data sets confirmed that soil compaction may play a crucial role in explaining nutrient cycling and plant community composition in natural grasslands. However, there is a need for field experiments directly investigating the relative importance of trampling-induced soil compaction for nutrient cycling along a gradient of soil types.

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